
INSECT FORAGERS ON *SOLANUM* FLOWERS IN AUSTRALIA¹

Gregory J. Anderson² and David Symon³

ABSTRACT

Eighteen native insect species were found on flowers of 18 Solanum species in a field study in Australia. All of the Solanum species studied are endemic to Australia, and about one-half of them are andromonoecious or dioecious. Fifteen of the insect species and 93% of total floral visitors were bees. New records of activity on Solanum flowers in Australia are reported for Braunsapis and Xylocopa (Anthophoridae), Leioproctus (Colletidae), and Trigona (Apidae). Two species each of the pollen-collecting bees Amegilla (Anthophoridae), Nomia (Halictidae), and Trigona are considered the most significant floral visitors. This conclusion is based on the distribution, abundance, and behavior of the bees, and on the high percentage of Solanum pollen in pollen loads. Amegilla and Nomia extract pollen by "buzzing" it out of the anthers; Trigona species do not. Species of Amegilla are hypothesized to effect interpopulation outcrosses. Trigona species are considered important primarily in self-pollination, and species of Nomia transmit pollen both within and between plants. This pollinator assemblage is postulated to have been associated with the evolution of dioecy in Australian Solanum.

Solanum flowers are of the "dish-bowl" type of Faegri & van der Pijl (1979) and as a consequence do not physically exclude floral visitors. However, these wide-open flowers do not represent the cornucopia to bees and other floral visitors that some other dish-bowl species do (e.g., *Tilia*, Anderson, 1976) because floral rewards are limited and there are specialized requirements for pollen extraction. Although extrafloral nectaries have been described in *Solanum*, floral nectar is absent (Anderson & Symon, 1985); and pollen, the only reward offered, is not easily accessible to all floral visitors. *Solanum* is the exemplar of the more than 540 genera whose anthers open by terminal pores rather than by longitudinal slits (Vogel, 1978; Buchmann, 1983). *Solanum* pollen is typical for species with poricidal flowers (Buchmann, 1983) in that it is relatively dry (not sticky) and has a smooth, granulate tectate exine (Anderson & Gensel, 1976). To remove pollen, floral visitors can either "milk" the anthers by stroking them from base to apex with their mandibles (e.g., Thorp & Estes, 1975), dig it out of the terminal pores, steal pollen by biting holes in the sides of the anthers (Buchmann, 1983), or buzz the pollen out of the terminal pores. Thorp

& Estes (1975) described buzz or vibratile pollination succinctly as "shivering the indirect flight muscles of the thorax while the wings [are] in repose." Buchmann (1983) estimated that about 60% of angiosperm species with poricidal anthers, including *Solanum*, are buzz pollinated.

The general syndrome of *Solanum* pollination, as described above, is well known. However, there is little known about specific pollinators and pollination. This is particularly true for Australia, where even some of the floral visitors are unknown (see below). Michener's (1965) major study of the bees of Australia reported collections of only three species from three genera on a single species of *Solanum* in southern Queensland. Symon's (1979) review of *Solanum* pollinators includes reports of seven taxa of bees. Armstrong's (1979) thorough overview of biotic pollination in Australia includes only one citation beyond Michener's and Symon's studies. Thus, we present information that expands the data base on *Solanum* pollinators. Also included is an analysis of insect pollen loads and relative abundance of insects on flowers to address the question of their importance as effective pollinators of *Solanum*. Finally, we speculate on the role of pollinators

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² Ecology and Evolutionary Biology U-43, University of Connecticut, Storrs, Connecticut 06268, U.S.A.

³ State Herbarium, North Terrace, Adelaide, South Australia 5000, Australia.

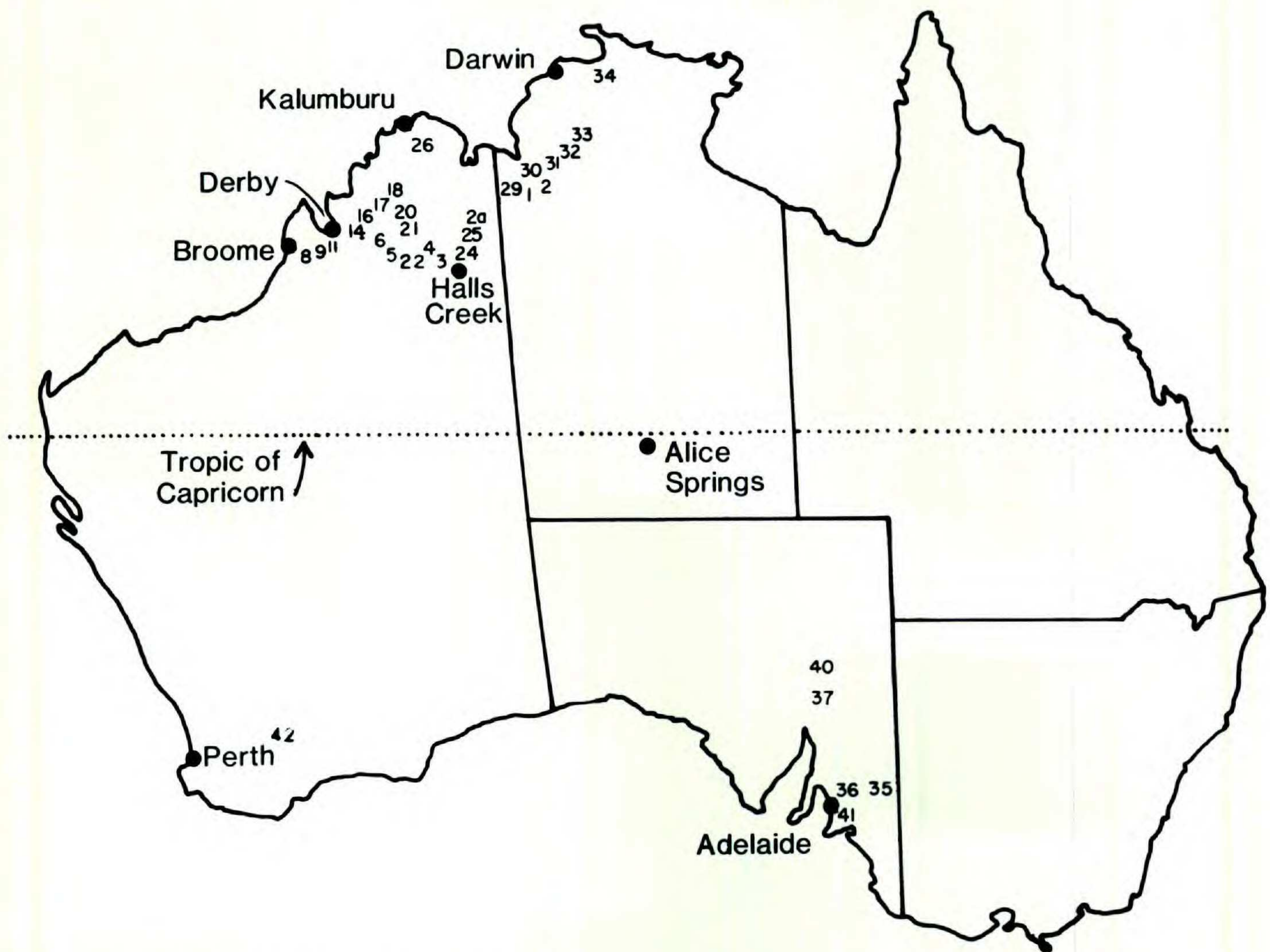


FIGURE 1. Field collections. Numbers correspond to the study areas cited in Appendix I.

in the evolution of nonhermaphroditic breeding systems.

METHODS

Insects were collected only from open *Solanum* flowers (i.e., not from the extrafloral nectaries) primarily from natural populations in 1979–1980. The study was centered on andromonoecious or dioecious solanums, the distribution and biology of which are given by Symon (1981). The species studied are as follows. The five-letter abbreviations are those used in Appendix I; the single letters indicate whether the species bears only hermaphroditic flowers (H), or whether it is andromonoecious (A) or dioecious (D): *Solanum asymmetriphyllum* Specht (asymm) (D), *S. beaugleholei* Symon (beaug) (A), *S. cinereum* R. Br. (ciner) (A), *S. cunninghamii* Bentham (cunni) (D), *S. dioicum* W. Fitzg. (dioic) (D), *S. diversiflorum* F. Muell. (diver) (A), *S. eburneum* Symon (eburn) (A), *S. ellipticum* R. Br. (ellip) (H), *S. esuriale* Lindley (esuri) (H), *S. hoplopetalum* Bitter & Summerh. (hoplo) (H), *S. leopoldense* Symon (leopo) (D), *S. lucani* F. Muell. (lucan) (H), *S. parvifolium* R. Br.

(parvi) (H), *S. petrophilum* F. Muell. (petro) (H), *S. quadriloculatum* F. Muell. (quadr) (H), *S. sturtianum* F. Muell. (sturt) (H), *S. tudununggae* (tudun) (D).

Because these *Solanum* species occur primarily in northern Western Australia and the Northern Territory, fieldwork was concentrated there. The study in this region ranged over some 5,000 km. Collections were also made in South Australia, including a small sample taken from garden-grown native plants in Adelaide, and from Western Australia (by R. Thorp). Flowers were open, and collections and observations were made throughout the daylight hours. Thousands of individuals were observed, but not all floral visitors were taken. After vouchers were taken within a given area, only observations of behavior were recorded. Specimens netted from flowers were stored with cotton in separate vials to prevent contamination of pollen loads. The plant species, time of day, and notes on insect behavior were recorded at each site. Pollen loads removed from insects were mounted on slides in aniline blue in lactophenol and analyzed for the percentage of *Solanum* pollen and the num-

TABLE 1. Summary by genus of insect visitors to *Solanum* flowers. See Appendix I for detailed information. * = see Discussion; others have reported vibratile activity.

	Num- ber of Species	Num- ber of <i>Sola- num</i> Species Visited	Num- ber of Locali- ties	% of Total Sample (indi- viduals)	Vibra- tile Pollen Re- moval	Sec- onds on Each Flower (range)	% Activity after Noon	% <i>Sola- num</i> Pollen in Pollen Load	Num- ber of Other Polleno- morphs
Infrequent floral visitors									
Diptera		2	3	5	no				
<i>Braunsapis</i>	1	2	2	< 1	no				
<i>Hylaeus</i>	2	1	1	< 1	no				
<i>Lasioglossum</i>	1	1	1	< 1	no*				
<i>Leioproctus</i>	1	1	1	< 1	no				
<i>Xylocopa</i>	1	1	1	< 1	yes				
Abundant floral visitors									
<i>Amegilla</i>	3	7	11	15	yes	1-3	5	79	1.1
<i>Nomia</i>	4	11	20	34	yes	1-10	9	79	1.1
<i>Trigona</i>	2	7	17	44	no	1-90	16	99	0.2

ber of other pollinomorphs. The fidelity to *Solanum* flowers was estimated from these calculations. Plant vouchers are in AD and insect vouchers in the collections of the Western Australian Museum in Perth.

RESULTS

INSECT DIVERSITY AND DISTRIBUTION

Specific data on time and place of collection and on pollen loads carried are presented in Appendix I, and the locations of the collection sites given there are plotted in Figure 1. The data from the Appendix are summarized in Table 1.

More than 150 insects, 93% of which were bees, were collected, representing at least 18 species in two orders (Appendix I). All of the bees were females except one *Amegilla pulchra* taken from *S. ellipticum* in South Australia. In addition to collections from Western Australia and the Northern Territory, a few individuals of *Nomia* and *Amegilla* were taken in South Australia. The following four bee genera are reported here for the first time from *Solanum* flowers in Australia: *Braunsapis*, *Leioproctus*, *Trigona*, and *Xylocopa*. The emphasis in the following analyses centers on the three most frequently collected genera: *Amegilla*, *Nomia*, and *Trigona*.

The collection sites (Fig. 1) of the three primary bee genera correspond to the general range of the solanums in the study area (Symon, 1981). As Table 1 shows, individuals of *Nomia* and *Trigona* were found at nearly twice as many sites as *Ame-*

gilla, and individuals of *Amegilla* were less abundant than either *Nomia* or *Trigona*. The two species of *Amegilla* were equally abundant and widespread; one species was more widely distributed and was locally abundant in *Nomia* (*N. flavoviridis*) and in *Trigona* (undescribed species "B"). While these data accurately reflect the rank-order of occurrence of the genera as we observed them in the field, the frequency figures are biased against *Nomia* and *Trigona*, which were much more abundant than reflected in the collections. *Trigona* was particularly abundant, with sometimes tens of individuals foraging over the flowers of a single plant.

FORAGING BEHAVIOR

As indicated in Table 1, *Amegilla*, *Nomia*, and *Xylocopa* were observed to vibrate or "buzz" the pollen out of the flowers; the remaining five bee genera were not. *Lasioglossum*, however, has been observed to buzz flowers in other studies (e.g., Bernhardt, 1986; Buchmann, 1983). Of the five genera not observed to utilize vibratile extraction, only *Trigona* was found on more than three occasions (Table 1); thus, the other four are not considered primary pollinators. Individuals of *Trigona* collect pollen from the anthers by digging it out of the terminal pores and by scavenging for it on floral parts such as the corolla and stigma (Fig. 2). No obvious differences in behavior were noted for insect visitors to hermaphroditic flowers, to staminate flowers of the andromonoecious species, or to the staminate or pistillate flowers of the dioecious species.



FIGURE 2. A *Trigona* (within circle) foraging on the stigma of a hermaphroditic flower of the andromonoecious *Solanum beagleholei*. The flower is about 30 mm in diameter.

The length of time individual bees stay on flowers is correlated with their size and capability to buzz flowers. The bees that vibrate pollen out of the flowers are generally larger (*Amegilla*—about 13 mm; *Nomia*—8–10 mm) and stay for only a short time (one to a few seconds) on each flower (Table 1). On the other hand, individuals of *Trigona* (smallest of the three species, about 5 mm) spent up to one minute on each flower. Individuals of *Trigona* frequently visited several flowers in the same inflorescence. This is in contrast with *Amegilla*, where an individual usually visits only a single flower per plant and then flies some distance, often away from the population under study. Individuals of *Nomia* most often foraged within and/or among inflorescences of the same population.

Most *Amegilla* visits take place before 10 A.M. (Table 1; Appendix I, column 5). The majority of visits by *Nomia* and *Trigona* also occur during this

period, but significant proportions of the individuals of these two genera are also active after noon.

INSECT FIDELITY

The average fidelity for all six major insect visitors (two species each from *Amegilla*, *Nomia*, and *Trigona*) is high (Table 1; Appendix I, column 3). For the genera overall, however, the fidelity estimate for *Trigona* is 20% higher than for either *Nomia* or *Amegilla*. These figures are, as one would expect, paralleled by the estimates of the number of other species visited (Table 1; Appendix I, column 4): *Nomia* and *Amegilla* pollen loads include about seven times as many other species as found in pollen loads of *Trigona*.

The pollen loads from the scopae or corbiculae respectively of the *Nomia* and *Trigona* were somewhat more sticky than those carried by *Amegilla*.

Amegilla scopae are covered with long hairs, among which the drier pollen loads were packed.

DISCUSSION

Solanum flowers present a relatively rich pollen resource for the bees that can exploit them. Although they lack nectar and restrict access to pollen (having only terminal anther pores), they are heavily visited by at least a few species. This is likely a tribute to their local abundance and the relatively large quantity of pollen available per flower (more than one million grains in some species, Anderson & Symon, in press). Although a range of insects was observed to visit the flowers, not all were considered significant pollinators (Table 1). Based on distribution and abundance over the range of the solanums, five of the bee genera and other insect groups are considered relatively insignificant pollinators, but these cannot be ruled out as occasional pollinators (see below). Two species each in *Amegilla*, *Nomia*, and *Trigona* are the primary floral visitors, and, as a consequence of this and their behavior, we propose that they are the major pollinators of the *Solanum* species studied.

Michener (1965) suggested that a large percentage of the Australian bees are oligolectic on the Myrtaceae but proposed that this is due largely to the overwhelming abundance of species in this family. In addition, he listed several genera, including *Nomia*, *Trigona*, and *Amegilla*, as examples of bees visiting a wide variety of species. In fact, some of the same genera of pollen-collecting bees (*Nomia*, *Trigona*, *Braunsapis*, *Xylocopa*) are reported as pollinators of another species from nearby Indonesia that is dioecious and offers only pollen as a reward, *Decaspermum parviflorum* (Myrtaceae) (Kevan & Lack, 1985). Although Michener (1965) did not treat the bee species we studied, this generalist behavior also likely applies to them. On the other hand, the proportion of *Solanum* pollen in pollen loads (79–99%) implies fidelity high enough to consider these polylectic genera to be important pollinators and to be temporally and spatially specialized on *Solanum*. This supports the contention by Thorp (1979) and Armstrong (1979) that most pollen-collecting bees show a high degree of diurnal or temporal constancy. Prance (1985) made a similar suggestion for polylectic bees from the Amazon rain forest.

Although the sticky pollen masses carried by individuals of *Nomia* and *Trigona* might indicate collection of nectar from other species (Thorp, 1979; Buchmann, 1983), the nearly monotypic nature of the loads (especially of the *Trigona*)

suggests that some other substance could be involved (perhaps stigmatic exudate, see below). Alternatively, the *Trigona* species could be moistening pollen loads with honey carried in their crops. Obviously nectar or honey from some source other than the *Solanum* flowers provides the carbohydrate resource to subsidize the pollen-collecting activities of the bees.

Nomia and *Amegilla* are ground-nesting, solitary, larger bees and are well represented in Australia (85 and 69 species, respectively; T. Houston, pers. comm.). These genera also share the ability to vibrate pollen out of the anthers. Michener (1965) indicated that the highly social, tree-nesting *Trigona*, although not as diverse in Australia (only about 14 species, T. Houston, pers. comm.), visits a wide range of monocots and dicots. However, this mostly tropical genus (Bernhardt, 1987) does not vibrate pollen out of the anthers and is too small to simultaneously contact stigmata while working anthers of a few of the large-flowered diclinous solanums.

Are species of *Trigona* then simply pollen thieves removing the reward without effecting pollination? In this instance, that conclusion does not seem warranted. We never observed them biting holes in anther bases to steal pollen, and anthers of dried voucher specimens do not have holes. Some individuals of *Trigona* opportunistically collect pollen spread over the flower, taking advantage of the activities of the vibratile pollinators. However, others are active on flowers not visited previously; we regularly observed them digging pollen out of the terminal pores of anthers. Members of *Trigona* were also observed foraging on stigmatic surfaces (Fig. 2). They may have been gathering pollen, but it is also possible that they were collecting stigmatic fluid to cement pollen grains together, as Baker et al. (1973) reported for other angiosperms. In either case, with such behavior they could effectively transmit pollen from anthers to stigmata in even the large-flowered species. Given this, and that *Trigona* species were omnipresent diurnally, were more abundant on *Solanum* flowers than all the other species combined, and showed 99% fidelity, we propose that these little bees are significant pollinators.

In view of the fact that representatives of *Trigona* tended to visit flowers in the same inflorescence, those on the same plant, or those within a population, we suggest that most often they effect self-pollination. This is reinforced by the colony behavior of social bees like *Trigona*, where individuals in various parts of a colony tend not to sample widely but continue to visit one area or

population repeatedly (T. Seeley, pers. comm.). Two features of the plants are relevant to this hypothesis as well. First, it is possible to self because most species of *Solanum* that have been studied (outside of the tuberous solanums and their relatives), including those from Australia, are self-compatible (Anderson & Symon, in press; Whalen & Anderson, 1981). Secondly, we observed that populations of most of the *Solanum* species studied are small in size and are widely separated from each other. These populations are even smaller (genetically) when one takes into account that most of the species reproduce vegetatively and form large clones, thus most of what appear to be genets in an area are actually ramets (Symon, 1981; Anderson & Stebbins, 1984; Anderson & Symon, in press). As a result, even many foraging visits between "plants" simply constitute visits to different ramets.

The largest but least abundant bees (*Amegilla*) visit flowers for only a very short time, supporting Buchmann's (1983) suggestion that the length of buzzing time is inversely correlated with bee size. These bees behave like "trap liners" (e.g., Janzen, 1971); that is, most visited only a single flower in an area and then flew off and out of sight, presumably to another *Solanum* flower (based on the nearly 80% purity of pollen loads). Such behavior supports the contention that *Amegilla* species are outcrossing agents transmitting pollen among genets. The bees in the first section of Table 1 were not abundant within any population at any site studied. Thus, if they are significant pollinators, they are also likely to effect outcrossing.

The *Nomia* species are intermediate between the small *Trigona* and large *Amegilla* in temporal pattern, abundance, size, visitation times, and behavior (Table 1). Individuals of *Nomia* visited more than one flower per plant and often visited other plants within the population before flying out of sight. As a consequence, we predict that these species generally effect inbreeding.

It seems that most flowers are visited, and observations of fruit set from the previous season showed a high seed set. Thus, we conclude that seed set is likely not pollen limited. Snow (1986) implied this is often the case for insect-pollinated species.

The nectarless flowers of *Solanum* may promote interplant or interpopulation foraging as suggested by Bernhardt (1987) for Australian *Acacia* (which also has no floral nectar). Bees collecting pollen have to find other species as nectar sources; this interruption raises the possibility of returning to a different plant or population of *Solanum*, thereby

increasing the chance of effecting outcrossing. On the other hand, given the population structure of the solanums and the pattern of visitation (especially that of *Trigona*), it is likely that more than three-fourths of interfloral visits result in self crosses. This strong likelihood lends strength to the arguments (Anderson & Stebbins, 1984; Anderson & Symon, in press) that dioecy, which promotes genetically wider crossing, may have been selected in response to several features of the hermaphroditic-flowered progenitors of the andromonoecious and dioecious species. These features include self-compatibility, vegetative reproduction, scattered population distribution, and the behavior of the pollinator assemblage as described herein.

This exclusive pollen-collecting behavior of insects on *Solanum* flowers has been accommodated in the Australian diclinous species. In both andromonoecious and dioecious species, all flowers are morphologically hermaphroditic (Anderson & Symon, in press). In staminate flowers of the andromonoecious and dioecious species the gynoecia are present but reduced. This reduction is presumably of little consequence to the pollen-collecting foragers. Of more importance is the fact that in the dioecious species the pistillate flowers bear anthers with pollen. This pollen reward differs from the usual tricolporate pollen of *Solanum* in that it is inaperturate (Anderson & Gensel, 1976). The inaperturate pollen is fully viable but incapable of germination (Levine & Anderson, 1986). Thus, the Australian dioecious species have a reward system that maintains pollinator visitation, but one that also disallows the self-pollination promoted by the plant biology and pollinator behavior.

LITERATURE CITED

- ANDERSON, G. J. 1976. The pollination biology of *Tilia*. *Amer. J. Bot.* 63: 1203-1212.
- & P. G. GENSEL. 1976. Pollen morphology and the systematics of *Solanum* section *Basarthrum*. *Pollen & Spores* 17: 533-552.
- & G. L. STEBBINS. 1984. Dioecy versus gametophytic self-incompatibility: a test. *Amer. Naturalist* 124: 423-428.
- & D. E. SYMON. 1985. Extrafloral nectaries in *Solanum*. *Biotropica* 17: 40-45.
- & ———. Functional dioecy and andromonoecy in *Solanum*. *Evolution* (in press).
- ARMSTRONG, J. A. 1979. Biotic pollination mechanisms in the Australian flora—a review. *New Zealand J. Bot.* 4: 467-508.
- BAKER, H. G., I. BAKER & P. A. OPLER. 1973. Stigmatic exudates and pollination. Pp. 47-60 in N. B. M. Brantjes (editor), *Pollination and Dispersal*. Department of Botany, Univ. Nijmegen, Nijmegen, Netherlands.
- BERNHARDT, P. 1986. Bee-pollination in *Hibertia fas-*

- ciculata* (Dilleniaceae). *Pl. Syst. Evol.* 152: 231–241.
- . 1987. A comparison of the diversity, density, and foraging behavior of bees and wasps on Australian *Acacia*. *Ann. Missouri Bot. Gard.* 74: 42–50.
- BUCHMANN, S. L. 1983. Buzz pollination in angiosperms. Pp. 73–113 in C. E. Jones & R. J. Little (editors), *Handbook of Experimental Pollination Biology*. Van Nostrand Reinhold, New York.
- FAEGRI, K. L. & L. VAN DER PIJL. 1979. *The Principles of Pollination Ecology*. Pergamon Press, New York.
- JANZEN, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171: 203–205.
- KEVAN, P. G. & A. J. LACK. 1985. Pollination in a cryptically dioecious plant (*Decaspermum parviflorum* (Lam.) A. J. Scott (Myrtaceae)) by pollen collecting bees in Sulawesi, Indonesia. *Biol. J. Linn. Soc.* 25: 319–330.
- LEVINE, D. A. & G. J. ANDERSON. 1986. Evolution of dioecy in an American *Solanum*. Pp. 264–276 in W. G. D'Arcy (editor), *Solanaceae: Biology and Systematics*. Columbia Univ. Press, New York.
- MICHENER, C. D. 1965. A classification of the bees of the Australian and South Pacific regions. *Bull. Amer. Mus. Nat. Hist.* 130: 1–362.
- PRANCE, G. T. 1985. The pollination of Amazonian plants. Pp. 166–171 in G. T. Prance & T. E. Lovejoy (editors), *Key Environments: Amazonia*. Pergamon Press, Oxford.
- SNOW, A. 1986. Pollen dynamics in *Epilobium canum* (Onagraceae): consequences for gametophytic selection. *Amer. J. Bot.* 73: 139–151.
- SYMON, D. E. 1979. Sex forms in *Solanum* (Solanaceae) and the role of pollen collecting insects. Pp. 385–397 in J. G. Hawkes, R. N. Lester & A. D. Skelding (editors), *The Biology and Taxonomy of the Solanaceae*. Linnean Society Symposium Series, 7. Academic Press, London.
- . 1981. A revision of the genus *Solanum* in Australia. *J. Adelaide Bot. Gard.* 4: 1–367.
- THORP, R. W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Ann. Missouri Bot. Gard.* 66: 788–812.
- & J. R. ESTES. 1975. Intrafloral behavior of bees on flowers of *Cassia fasciculata*. *J. Kansas Entomol. Soc.* 48: 175–184.
- VOGEL, S. 1978. Evolutionary shifts from reward to deception in pollen flowers. Pp. 89–96 in A. J. Richards (editor), *The Pollination of Flowers by Insects*. Linnean Society Symposium Series, 6. Academic Press, London.
- WHALEN, M. D. & G. J. ANDERSON. 1981. Distribution of self-incompatibility and infrageneric classification in *Solanum*. *Taxon* 30: 761–767.

APPENDIX I. *Insects on Solanum flowers. See Methods for full names and authorities for the Solanum species. sp. = species not identified, s.n. = without number, * = plant cultivated.*

Insects	<i>Solanum</i> Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Captured	Study Site (see Fig. 1)
Bees						
Anthophoridae						
<i>Amegilla (Amegilla) aeruginosa</i> (Smith)	cunni	341			7:00	8
		348			7:00	8
	dioic	369	100	0	7:30	18
	eburn	300	72	1	9:30	1, 2
		301	69	1	9:30	1, 2
		304			8:30	30
		305			8:30	30
		435	100	0	8:30	30
		436			8:30	30
		437			8:30	30
		438	87	1	8:30	30
			$\bar{X} = 85$	$\bar{X} = 0.8$		
	<i>A. (Amegilla) pulchra</i> (Smith)	diver	306	37	3	15:00
313			37	2	9:30	3
398				3	7:30	2a
ellip		460	100	0	15:00	37
		416	100	0	15:00	37
		472	100	0		40
esuri		457				41
hoplo		s.n.				42
sturt		s.n.				37
sp. ?*		474				41
		$\bar{X} = 73$	$\bar{X} = 1.33$			
<i>A. sp.?</i>	dioic	363			9:00	16
		364			9:00	16
<i>Genus (Amegilla)</i>			$\bar{X} = 79$	$\bar{X} = 1.09$		11 sites
<i>Braunsapis sp. ?</i>	dioic	351	100	0	8:00	14
	eburn	450			10:30	31
<i>Xylocopa (Koptortosoma) aruana</i> Ritsema	eburn	444	99	1	10:30	31
Apidae						
<i>Trigona (Plebeia) sp. A</i>	cunni	344			7:00	8
		345			7:00	8
		346			7:00	8
		347			7:00	8
	dioic	383	100	0	11:00	21
		384	100	0	11:00	21
	diver	393	100	0	7:30	2a
		396	100	0	7:30	2a
	lucan	408			9:00	24
		409			9:00	24
		410			9:00	24
		411			9:00	24
		412			9:00	24
		413			9:00	24
		414			9:00	29
		415	100	0	9:00	24
		416	100	0	9:00	24
417		100	0	9:00	24	

APPENDIX I. *Continued.*

Insects	<i>Solanum</i> Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Cap- tured	Study Site (see Fig. 1)
	quadr	418			11:00	25
		419			11:00	25
			$\bar{X} = 100$	$\bar{X} = 0$		
<i>Trigona (Plebeia) sp. B</i>	beaug	370			9:00	20
		371			9:00	20
		372			9:00	20
		373			9:00	20
		374			9:00	20
		375			9:00	20
		376	99	1	9:00	20
	dioic	326	100	0	15:00	6
		327	100	0	15:00	6
		328			15:00	6
		329			15:00	6
		330			15:00	6
		352	100	0	9:00	16
		353	100	0	9:00	16
		354			9:00	16
		355			9:00	16
		368			12:00	17
		382			11:00	21
		385	100	0	11:00	21
		386	100	0	11:00	21
	diver	307				
		308	100	0	9:30	3
		309	96	1	9:30	3
		310			9:30	3
		311			9:30	3
		312			9:30	3
		324	100	0	10:00	5
		325	100	0	10:00	5
		394	100	0	7:30	2a
		395	100	0	7:30	2a
		397	90	1	7:30	2a
		400			7:30	2a
		401			7:30	2a
	eburn	303	99	1	10:00	2
		429			15:30	29
		430	100	0	15:30	29
		439	100	0	8:30	30
	lucan	337			15:00	9
		451	100	0	11:30	32
		452			12:30	33
		453			12:30	33
		454	100	0	12:30	33
			$\bar{X} = 99$	$\bar{X} = 0.22$		
			$\bar{X} = 99$	$\bar{X} = 0.16$		
Genus (<i>Trigona</i>)						17 sites
Colletidae						
<i>Hylaeus (Prosopistemon) sp. 1</i>	cunni	334			12:00	8
		335			12:00	8
<i>H. (Rhodohylaeus) sp. 2</i>	cunni	336	95	1	12:00	8
<i>Leioproctus (Leioproctus) sp.</i>	hoplo	s.n.				42

APPENDIX I. *Continued.*

Insects	<i>Solanum</i> Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Captured	Study Site (see Fig. 1)
Halictidae						
<i>Lasioglossum</i> sp.	leopo*	459	79	2	10:00	36
	parvi*	<i>s.n.</i>				36
<i>Nomia (Austronomia) dimissa</i> (?) Cockerell	beaug	380	93	1	9:00	20
<i>N. (Austronomia) flavoviridis</i> Cockerell	beaug	379	83	1	9:00	20
		381	100	0	9:00	20
	ciner*	<i>s.n.</i>				36
	dioic	315	75	2	11:00	4
		331	100	0	10:00	6
		332	99	1	10:00	6
		358	100	0	9:00	16
		359	100	0	9:00	16
		360	100	0	9:00	16
		361	65	1	9:00	16
		362	50	2	9:00	16
	diver	317	95	2	10:00	5
		318	98	2	10:00	5
		319	54	2	10:00	5
		320			10:00	5
		321			10:00	5
		322			10:00	5
	eburn	431	100	0	15:30	29
		432	83	1	15:30	29
		433	39	2	15:30	29
		434	84	1	15:30	29
		446	65	1	10:30	31
		447	9	1	10:30	31
		448	10	1	10:30	31
		449	13	3	10:30	31
	ellip	<i>s.n.</i>				37
	esuri	458			14:00	35
	lucan	407	100	0	9:00	24
		455	34	3	12:30	33
	petro	<i>s.n.</i>				37
	quadr	420			11:00	25
		421	99	1	11:00	25
		422	100	0	11:00	25
	sturt	473	100	0		40
	tudun	428	100	0	11:00	26
			$\bar{X} = 78$	$\bar{X} = 1.0$		
<i>N. (Hoplonomia) rubroviridis</i> Cockerell	cunni	342	33	1	7:00	8
		343	46	3	7:00	8
		349	98	1	12:30	11
	eburn	302	73	2	10:00	2
	lucan	402	97	2	9:00	24
		403	99	1	9:00	24
		404	100	1	9:00	24
			$\bar{X} = 80$	$\bar{X} = 1.6$		
<i>N. sp. ?</i>	dioic	387	99	1	10:00	22
		388			10:00	22
		389			10:00	22

APPENDIX I. *Continued.*

Insects	<i>Solanum</i> Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Cap- tured	Study Site (see Fig. 1)
		390			10:00	22
	diver	314	37	2	9:30	3
Genus (<i>Nomia</i>)			$\bar{X} = 79$	$\bar{X} = 1.14$		20 sites
Floral Visitors Other than Bees						
Eumenidae (Hymenoptera)	asymm	456	94	0		34
Ants	dioic	333			15:00	6
Diptera	quadr	423-427			10:00	25
	cunni	338			7:00	8
		339			7:00	8